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The occurrence of non-territorial adult and yearling males on the mating ground in the Pipistrelle bat *(Pipistrellus pipistrellus)*

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Abstract

Male pipistrelle bats set up individual territories at special mating grounds around their roosts. The occurrence of surplus males, non-territorials, indicates that the population density of males at the mating ground is limited by the number of roost sites and the territorial behaviour of the residents. The silence and sporadic appearence of the non-territorial males, and their response to high female densities, support the hypothesis that these males may try to steal matings from territory owners.

Immature male yearlings were excluded from the roosts of territorial males to the same degree as non-territorials. The high frequency by which yearling males return to the same roost makes them potential competitors for the territories. The relatively high percentage of returning male yearlings which become owners of a territory supports this hypothesis. The low recovery rate of non-territorials probably results from their failure to get established.

Introduction

In the pipistrelle bat (*Pipistrellus pipistrellus* Schreber, 1774), as in most temperate vespertilionids, there is a sex difference in dispersal after hibernation (Bradbury 1977). The sexes remain in unisexual units until late summer when mating groups are formed. In late spring, when fertilization by stored sperm takes place (Pagenstecher 1859), females aggregate at traditional roosts to form nursing colonies (e.g. Ryberg 1947; Hůrka 1966; Stebbings 1968; Grimmberger and Bork 1978; Swift 1980). At the same time, adult males arrive at the mating grounds. Here, mating grounds are defined as an area where males traditionally establish territories around their roost sites (in this case bat boxes). The males monopolize these roost sites until the end of the mating season. Following Kaufmann (1983), territory is defined as "space-related dominance" where the territory owner has priority of access to critical resources.

The young are born in mid June. After weaning at the end of July – earlier or later according to local climatic conditions – the mating period starts. Females attain sexual maturity in their first autumn (Racey 1974) and both adult and juvenile females aggregate at the mating ground, where they form harem groups. Mating activities decrease by the end of September. Pipistrelle males reach sexual maturity at an age of one year. The mating system of the pipistrelle bat has been described as a resource-defence polygyny, where the males control access to roost sites which are crucial for acquiring females (Gerell and Lundberg 1985; Lundberg and Gerell 1986).

Non-territorial adult and yearling males occasionally visit the mating grounds. In this paper the spatial and temporal distribution of non-territorial and yearling males in relation to that of territory holders is analysed.

Material and methods

The pipistrelle population, which is the subject of this paper, has been studied since 1981 using bat boxes. The study area is a 150-ha pine plantation 30 km east of Lund in southernmost Sweden. The boxes (Gerell 1985) were grouped (2–4) at spatially separated stations, in all 22 during 1981–1983 and 33 during 1984–1987. The spacing between stations varied between 75 and several hundred metres. Each station functioned as the territory of a single male and contained a number of alternative roost sites (boxes). The boxes were checked throughout the season (March–November), but more regularly from April to the end of September. Captured pipistrelles were sexed, aged and banded. Body mass was determined to the nearest 0.25 g with a Pesola spring balance, while forearm length was measured to the nearest 0.1 mm with dial calipers. Ageing and assessment of reproductive status were done according to Racey (1974). Juveniles were recognized by the presence of unfused and translucent phalangeal epiphyses. Immature males were distinguished from adult males by their tunica vaginalis, which is densely pigmented and can be seen through the skin. A yearling is here defined as an animal that is born during the immediately preceeding breeding period. Hence, the category yearling includes juveniles, immatures and males undergoing puberty.

In order to be classified as non-territorial, a male had to be sexually mature and known not to have established a territory in the area. Male yearlings were about two months old when they left their natal area and first appeared at the mating ground. Male juveniles found in maternity colonies are excluded from the following analysis.

Ultrasonic detectors; QMC S 100 (QMC Instrument Ltd.) and a D-940 (Ahlén et al. 1984), were used for identifying the sounds of the bats.

Results

Time of occurrence and location of non-territorial and yearling males in relation to territory holders

A. Non-territorial males

The number of non-territorial males visiting the stations per season ranged from 6 to 19 ($\bar{x}$ = 10.3, S.D. = 4.7, n = 72). The visiting frequency peaked in June–Sept. (Table 1). No significant difference was found between the number of non-territorials found alone at a

Table 1. **Number of non-territorial males and male yearlings caught during the period March–November in bat boxes at Vombs Fure, southern Sweden, 1981–1987**

	Non-territorial males		Male yearlings	
	n	%	n	%
Mar	2	2.2	–	–
Apr	8	8.6	–	–
May	8	8.6	–	–
Jun	15	16.1	–	–
Jul	17	18.3	–	–
Aug	22	23.7	25	18.1
Sep	13	14.0	78	56.5
Oct	5	5.4	30	21.7
Nov	3	3.2	5	3.6
Total	93		138	

station and found at a station occupied by a territorial male (χ^2 = 2.26, $p > 0.10$, df = 1, Table 2). Most of the visiting non-territorial males, however, were caught at roost sites unoccupied by territorial males (χ^2 = 22.89, $p < 0.001$, df = 1). In 1984 when the number of non-territorial males was high, their occurrence was positively correlated with the density of females (r_s = 0.62, df = 10, $p < 0.05$).

Table 2. **Number of non-territorial males (NT) and male yearlings (Y) captured at an unoccupied station, at the same station as a territory holder, and at the same roost as a territory holder**
Combined data from 1982–1987

	Unoccupied station		Station with territory holder		Same roost as a territory holder	
	NT	Y	NT	Y	NT	Y
Apr	2	–	1	–	5	–
May	4	–	1	–	3	–
Jun	11	–	3	–	0	–
Jul	11	–	5	–	1	–
Aug	9	12	7	9	1	2
Sep	9	34	2	28	2	16
Oct	4	17	0	2	0	0
Total	50	63	19	39	12	18

B. Male yearlings

The number of male yearlings banded per season ranged from 8 to 24 ($\bar{x}$ = 14.9, S.D. = 5.3, n = 104) and most of them were caught in September (Table 1). More than half of them (52 %) were captured at a station lacking a territorial male, 32 % at the same station as a territory holder, and 15 % at the same roost as a territorial male. Most of the yearlings, however, were found at unoccupied roosts (χ^2 = 33.50, $p < 0.001$, df = 1) (Table 2). Male yearlings did not appear more often than non-territorials at stations occupied by territorials (χ^2 = 2.16, df = 1, $p > 0.10$).

Recovery frequency

A. Non-territorial males

A total of 55 non-territorial pipistrelle males were banded during the period 1981–1986 (Table 3), of which only 6 were recaptured during consecutive years. One of them was recovered at the station where he was banded. In contrast, territorial males, showed a high rate of recapture and total roost-site fidelity.

Table 3. **Number of territorial, non-territorial and yearling males banded at Vombs Fure and recaptured in a succeeding year**
Combined data from 1981–87

	Number banded	Recaptures		
		n	%	at banding site (%)
Territorials	49	28	57.1	100.0
Non-territorials	55	6	10.9	16.7
Yearlings	80	24	30.0	66.7

In a particular season, the majority of non-territorial males were captured only once (Table 4). Data from the mating season only show the same pattern (76 % single captures).

B. Male yearlings

During the years 1981–1986 a total of 80 male yearlings were banded of which 24 returned to the study area during consecutive years (Table 3). Sixteen of these, now almost one-year old, were recaptured at the station where they were banded.

Table 4. **Number of times (%) non-territorial and yearling males were captured in the same season at Vombs Fure**
Combined data from 1981–87

	Capture frequency (times)		
	1	2	3
Non-territorials	50 (70.4)	18 (25.4)	3 (4.2)
Male yearlings	69 (71.9)	24 (25.0)	3 (3.1)

During a particular season most of the male yearlings were observed only once (Table 4). There was no difference in the number of times they were caught during the year of banding between those yearlings that returned the following season and those that did not ($\chi^2 = 1.50$, $p > 0.2$, $df = 1$).

Chance of becoming a territory holder

Only 4 % of the non-territorial banded during 1981–1986 later became territory holders in the study area, while the corresponding figure for the yearlings was 21 %. Of those that returned to the area no less than 71 % became owners of a territory compared with 33 % of the non-territorials.

Size and relative age of non-territorial males

A comparison of forearm length between territorial and non-territorial males showed that there was no significant difference in size between these two groups ($t = 0.93$, $p > 0.2$, $df = 102$). To determine whether territorial males were relatively heavier than non-territorials at the time of establishment, the ratio body mass : forearm length was compared between the two groups; the same comparison was also done for the mating season. During establishment no difference was found ($t = 0.19$, $p > 0.5$, $df = 38$), but during the mating period

Table 5. **Age distribution of captured non-territorial males (NT) and territorial males (T) during 1982–1986**

	Age class (years)					
	1		⩾1		⩾2	
	NT	T	NT	T	NT	T
1982	1	1	5	9	0	6
1983	0	2	8	10	2	5
1984	9	11	6	5	2	13
1985	4	3	3	4	0	9
1986	1	2	3	11	1	6
Total	15	19	25	39	5	39
χ^2	0.24		1.55		15.44	
p	>0.50		>0.20		<0.001	

non-territorial males were significantly heavier than territorial males ($t = 4.76$, $p < 0.001$, $df = 80$).

Comparison of the proportions of territorial and non-territorial males belonging to each of the age classes one year, and two years or older (Table 5), shows that territorials were significantly older than non-territorials ($\chi^2 = 10.79$, $p < 0.001$, $df = 1$).

Discussion

Most of the non-territorial males which visited the study area appeared on just a single occasion. Those that were caught more than once were never found at the same station twice. It may be interpreted that these males tried to get established in the area, but were prevented from occupying territories by the presence of residents. The very few occasions when a non-territorial male succeded in getting a territory occurred when a territory holder disappeared for some reason, or when excessive roost sites were provided (Lundberg and Gerell 1986). Thus, the density of the male population in the study area seems to be limited by the number of roosts and territorial behaviour.

The visiting frequency of non-territorials was highest in the period June–Sept. Spermatogenesis in pipistrelles is initiated in late spring (Racey and Tam 1974), and the males establish their territories in June. The relatively high number of non-territorial males recorded in the area before the females arrived (beginning of August) indicates that they compete for territories. Their still higher visiting frequency in August is probably related to the mating season. The search for females may result in an increased mobility of non-territorial males. The sound of advertising territorial males (Lundberg and Gerell 1986) may not only attract females but also non-territorial males.

In polygynous mating systems there is intense competition for mates, and the mating success varies between males. Most females are monopolized, and probably fertilized, by territory owners (Dewsbury 1982). Non-territorial or subordinate males often have developed alternative mating behaviours either as "satellites" (e.g. Hogan-Warburg 1966; Emlen 1976; Howard 1978; Perill et al. 1978; Wirtz 1982) or as "sneakers" (e.g. Le Boeuf 1974; Cluttonbrock et al. 1979; Gross 1982). The satellite tactic, where subordinates are associated with territory holders, does not apply to the pipistrelles studied. Non-territorial males were never observed to perform a song flight, the display by which territorial pipistrelle males attract females to their roost sites (Lundberg and Gerell 1986). Their silence, sporadic appearence, and response to high female densities suggest that non-territorial males try to make the best out of a bad situation functioning as sneakers, which (unnoticed) try to steal matings with the females of the territory holders.

There was no difference in size between non-territorial and territorial males. The dominance of the territory owners over non-territorial males is probably a result of both an age-related and an owner-intruder assymmetry. The lower body mass of territorial males during the mating period is caused by mating activities (Lundberg and Gerell 1986; Lundberg 1989). The relatively high body mass of non-territorial males during the mating season indicates that they really are non-territorial, and not just occasional visitors established elsewhere. It also shows that non-territorial males invest in survival rather than reproduction (Lundberg 1989).

In our pipistrelle bats, as in many mammals (Greenwood 1980), males tended to disperse while females remained mainly in their natal area. Both yearling females and males visited the study area during the mating period, but male yearlings appeared on average later (Gerell and Lundberg 1985). Studies on pipistrelle maternity colonies (Stebbings 1968; Rakhmatulina 1972; Swift 1980; Racey and Swift 1985) show no difference in development and time of leaving the colony between male and female yearlings. An explanation of the late arrival of the male yearlings to the mating ground could be the competition for unoccupied roost sites with non-territorial males.

Yearlings were excluded from territorial males' roosts to the same degree as the non-territorial males. Male yearlings cannot interfere with territorial males' chances to mate, so why do the latter bother to exclude these immature males? Yearling males may be prospecting for territories for future mating seasons. The high frequency by which yearlings return to the same roost, and their high success in getting territories, support this hypothesis. So, territory owners may make a future investment by excluding them.

The higher rate of recovery of yearlings compared with that of non-territorials may be explained by the difference in age. The probability of a yearling getting established is rather high compared with that of a non-territorial which has already failed. A better option for the latter is to visit other mating grounds, of which they already may have knowledge. Yearlings on the other hand return to the only area with which they are familiar.

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Zusammenfassung

Das Auftreten von nicht-territorialen erwachsenen und jungen Männchen im Fortpflanzungsrevier der Zwergfledermaus (Pipistrellus pipistrellus)

Männliche Zwergfledermäuse bauen individuelle Territorien in bestimmten Fortpflanzungsrevieren auf. Ihre Quartiere liegen innerhalb dieser Territorien. Das Auftreten von zusätzlichen, nicht-territorialen Männchen zeigt, daß die Populationsdichte der Männchen im Fortpflanzungsrevier durch die Anzahl der Quartiere und durch das Territorialverhalten der Revierinhaber begrenzt wird.

Die fehlenden Lautäußerungen und das sporadische Erscheinen nicht-territorialer Männchen und ihre Reaktion auf hohe Weibchendichte unterstützen die Hypothese, daß sich diese Männchen in schon besetzte Territorien einschleichen und sich dort vermutlich verpaaren.

Immature männliche Jungtiere wurden im selben Maß wie die nicht-territorialen Männchen aus den Quartieren der territorialen Männchen vertrieben. Da die Jungtiere sehr häufig zum selben Quartier zurückkehren, werden sie zu potentiellen Konkurrenten um die Territorien. Der relative hohe Prozentsatz zurückkehrender männlicher Jungtiere, die dann Inhaber eines Territoriums werden, unterstützt diese Annahme. Die geringe Wiederfangquote von nichtterritorialen Männchen ist wahrscheinlich dadurch bedingt, daß es ihnen im Gegensatz zu den männlichen Jungtieren nicht gelingt, sich zu etablieren.

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